

BEHAVIORAL CHARACTERS WITH SYSTEMATIC POTENTIAL IN STONEFLIES (PLECOPTERA)

DAVID D. ZEIGLER AND KENNETH W. STEWART

(DDZ) Department of Biology, Southwest Texas State University, San Marcos, Texas 78666; (KWS) Department of Biological Sciences, North Texas State University, Denton, Texas 76203.

Abstract.—Based on rapidly accumulating knowledge of drumming, a complex intersexual vibrational communication system in stoneflies, we propose and discuss several behavioral characters that may provide input for phenetic and/or cladistic analysis, including: (1) ability to drum (non-drumming, drumming), (2) signal type (sequential, grouped), (3) phasic structure of sequential signals (monophasy, diphasy), and (4) mode of vibration production (tapping, rubbing, tremulation). The more complex variations of signal structure (diphasy, grouping, rubbing, tremulation) appear to be derived when known species in various taxa of the suborder Arctoperlaria are tested by out-group comparison. Male-call diphasy and signal production by rubbing are derived among genera of Peltoperlidae and Perlidae, as are grouped signals in the family Perlodidae, and tremulation in the Chloroperlidae. Other finer aspects of drumming exchange or signal structure such as complex exchange structure, a large number of beats/signal, and non-constant beat intervals likewise appear to be apomorphic in contrast to extant simpler states in each category.

The potential for innate behavior to provide lines of evidence for systematic and phylogenetic analysis has long been recognized (Mayr, 1958; Ross, 1974). Behavioral systems suitable for such use have been identified and quantified in several insect groups including the Gryllidae (Alexander, 1962; Otte and Alexander, 1983) and the Chrysopidae (Henry, 1984). Recent studies have shown that the drumming behavior of stoneflies (Plecoptera) seems to offer a similarly useful behavioral system since it is relatively stereotyped at the species level, is most likely a homologous category of behavior, and has evolved into considerably diverse and complex patterns within the order (Stewart and Zeigler, 1984a; Maketon and Stewart, 1984; Zeigler and Stewart, 1985). Zwick (1973) suggested non-drum-

ming and drumming as ancestral and derived characters, respectively, separating the suborders Antarctoperlaria and Arctoperlaria. Nelson (1984) concluded, after a reassessment of 113 mostly morphological characters (but including drumming vs. non-drumming), using a computerized version of the Wagner Parsimony Method, that the available characters were insufficient for resolving phylogenetic relationships in the Plecoptera. He strongly suggested that the acquisition of additional characters would significantly increase our understanding of Plecoptera phylogeny.

We have concentrated over the past ten years on elucidating the nature of drumming in North American Arctoperlaria species in part to establish a behavioral data base for phylogenetic applications. A pre-

liminary assignment of polarity was made for certain drumming characters by Stewart and Zeigler (1984b). It is our objective in this paper to further define and better delineate pair-forming characters that appear to be potentially useful for phylogenetic analysis, and to give additional examples of preliminary character polarity testing using out-group comparison (Watrous and Wheeler, 1981).

THE NATURE OF DRUMMING AND SOME PROBLEMS OF RECENT QUANTITATIVE STUDIES

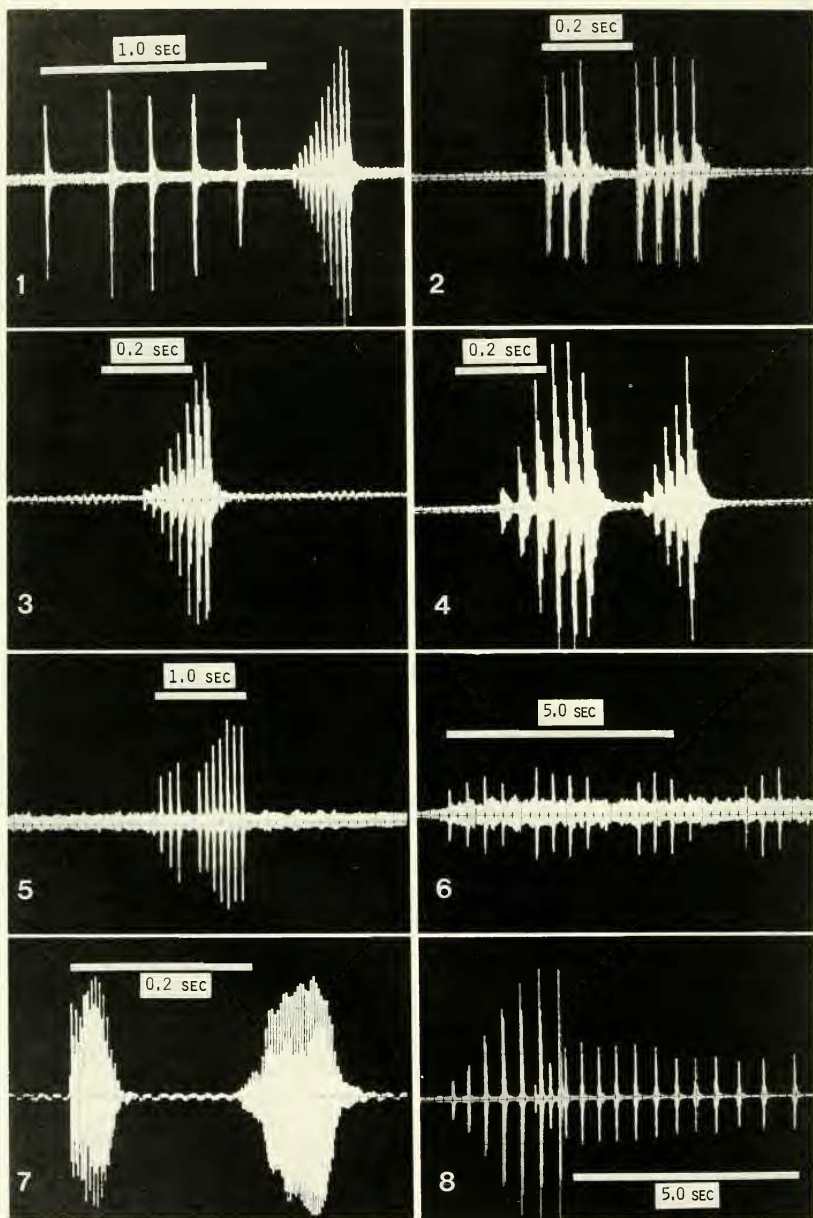
Stonefly drumming is an intersexual communication behavior for mate identification and location. The principal mode of drumming exchange involves substrate-borne vibrations produced when the insects strike or rub the substratum with the posteroventral portion of the abdomen (Rupprecht, 1967; Maketon and Stewart, 1984), although some species have been found to tremulate without abdomen/substratum contact (Rupprecht, 1981). The number and spacing of the resultant pulses provide the necessary information for species and sex recognition. Both sexes typically drum, and one or both partners search between drumming exchanges until tactile contact is established. Mating follows immediately.

These generalizations are based on the descriptions and quantitative data collected over the last twenty years, before which only a few qualitative descriptions were available. Some of these works have stressed characters such as signal duration (Zeigler and Stewart, 1977; Rupprecht, 1982) and beat frequency in beats/sec (Rupprecht, 1967; Szczytko and Stewart, 1979) which have limited usefulness, even as species level descriptors. Signal duration is a continuous variable which is affected by temperature (Zeigler and Stewart, 1977) and also by the number of beats/signal which can vary even at the individual level. Beat frequency may be useful (at noted temperatures) where the signal consists of a series of evenly spaced

beats, but the signals of many species have increasing or decreasing beat intervals or varying phasic structure (see diphasic calls below) which render a beat frequency value essentially useless in describing signal structure. Similar problems are inherent in the " \bar{x} beat interval" which is an average of all beat intervals in a signal. What is needed are drumming characters with few character states which will be useful in categorizing genera and families and for which character polarity can be tentatively determined. Following are several characters which look promising in these respects.

DRUMMING CHARACTERS THAT MAY PROVE USEFUL IN SYSTEMATIC STUDIES

Drumming vs. non-drumming. — This character has been used by Zwick (1973) and Nelson (1984), and indeed it should be very important except for two problems. First is the question of non-drumming. Most often drumming is observed and recorded under laboratory conditions that facilitate uniformity, increase efficiency of research time, and increase recording quality, all of which are difficult to accomplish in the field. If individuals fail to drum under laboratory conditions, we cannot necessarily assume that they are non-drummers in nature. Physical or temporal requirements or cues may limit or prevent drumming behavior under laboratory conditions. *Hydroperla crosbyi* (Needham and Claassen) was believed to be a non-drummer until more thorough observations proved otherwise (Zeigler and Stewart, 1985). A species must be observed in large numbers and at various ages under "natural conditions" over a 24 h period(s) in order to realistically determine its ability and/or tendency to drum. Consequently, Zwick (1973) and Nelson (1984) actually misused this character since Zwick's non-drumming *Antarctoperlaria* and Nelson's non-drumming families have either been inadequately investigated or not studied at all in terms of drumming capability.



Secondly, it is possible that some species may have secondarily lost drumming in favor of some other mate-location mechanism such as pheromones or specialized searching behavior so that, although originally considered primitive (Stewart and Zeigler, 1984b), in some cases non-drumming might be viewed as a derived trait. This will be a difficult question to resolve until a broader spectrum of data is available for the various families in both suborders.

Signal phase structure.—Males of many species produce what have been termed diphasic calls. Originally these calls were considered to have two “phases” or beat groupings with distinctively different temporal structure (beat spacing) in the two phases (Fig. 1). The category could also be extended to include calls of two beat groupings with similar beat spacing in the two beat groupings as in *H. crosbyi* (Fig. 2). It is certainly possible that as the calls of more species are recorded and described, the distinction between these two types will fade. However, both types of diphasic calls must logically be considered as derived in contrast to the simpler monophasic call (Fig. 3) typical of most species (Stewart and Zeigler, 1984b). To date, diphasic signal structure has not been found in the male calls of the Taeniopterygidae, Capniidae, or Pteronarcyidae, nor in the female signals of any family.

The origin of diphasic calls can be hypothesized from observations on available data. In the genus *Soliperla* (Peltoperlidae), males of *S. quadrispinula* (Jewett) and *S. thyra* (Needham & Smith) have simple monophasic calls while *S. fenderi* (Jewett) males have a derived diphasic call with distinctively different beat spacing in the two

phases. It could be hypothesized, judging from the similarity of *S. thyra*'s call and the second phase of *S. fenderi*'s call (Figs. 1, 3), that the *fenderi* call has been produced by adding a few widely spaced beats (apomorphic phase) before the original monophasic call sequence (plesiomorphic phase). Stark (1983) found that *S. quadrispinula* and *S. thyra* share many key morphological characters which distinguish their common recent lineage from that of *S. fenderi*'s.

Another possible origin of diphasic calls could be from simply repeating the original monophasic call sequence twice in rapid succession. The diphasic calls of *Kathroperla perdita* (Banks) are suggestive of this hypothesis (Fig. 4) as are those of *Isoperla gortzii* Illies (Rupprecht, 1969).

Finally, a diphasic call could originate by the dropping of one or more beats from the middle of a long monophasic call. Some calls from “fatigued” males of *Taeniopteryx burksi* Ricker & Ross (Fig. 5) showed missing beats resulting in a call of two distinct beat groupings (personal observation), and the typical call of *H. crosbyi* (Fig. 1) is suggestive of a monophasic call missing two internal beats. However, if interspecific call differences are in part the result of sexual selection, as is currently suggested (Thornhill and Alcock, 1983; West-Eberhard, 1983), this latter possibility is perhaps least likely since such calls would initially be received as “deficient” aberrations of the typical call.

Grouped calls.—Male calls of three or more beat groupings have so far been observed only in the family Perlodidae, and they appear to be derived (Fig. 9) when tested by out-group comparison (Watrous and

Figs. 1–8. Oscillographs of assorted plecopteran drumming signals. 1, Diphasic male call of *Soliperla fenderi*, 22°C. 2, Diphasic male call of *Hydroperla crosbyi*, 24°C. 3, Monophasic male call of *Soliperla thyra*, 24°C. 4, Diphasic male call of *Kathroperla perdita*, 23°C. 5, A male call of *Taeniopteryx burksi* showing a deleted 4th beat (after 25 min of male-female drumming contact). 6, Grouped male call of *Isonoides zionensis*, 22°C. 7, Rubbing male call of *Doroneuria baumanni*, 22°C. 8, Overlapping male-female drumming exchange of *Pteronarcys princeps*, 23°C.

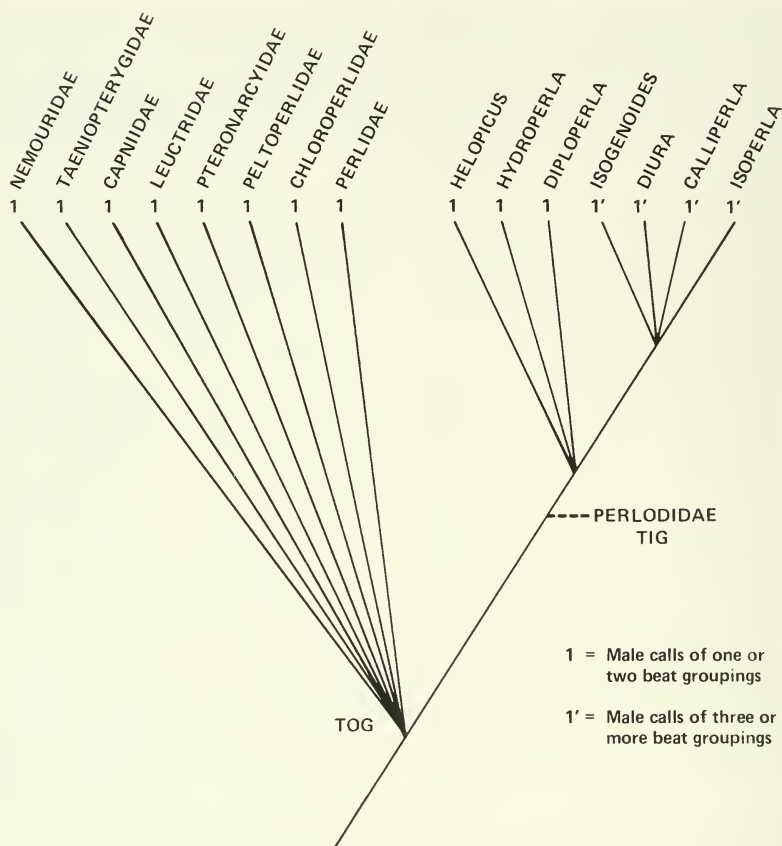


Fig. 9. Out-group comparison for male calls of three or more beat groupings (TOG = taxonomic out-group, TIG = taxonomic in-group).

Wheeler, 1981). These calls often appear to be closely spaced repetitions of an ancestral monophasic call. Evidence to support this view is best illustrated by *Isogenoides zionensis* Hanson in which the first few calls in a male-female exchange are grouped calls of three or four groupings (Fig. 6), but as exchanges continue, the male shifts to a simpler monophasic call which is very similar to a single beat grouping within the initial grouped calls (Stewart and Zeigler, 1984a).

Beating, rubbing, and tremulation.— There are at least three methods of signal production in the Plecoptera. Most commonly a pulse is produced as the abdomen strikes (beats) the substratum. Maketon and Stewart (1984) found that several perlids rub or scrape the substratum with their abdomen producing a distinctly different type of vibrational signal (Fig. 7). This manner of signal production seems to be a derived character state in the family Perlidae

(Maketon and Stewart, 1984), although rubbing has apparently arisen separately in some of the peltoperlids as well (Maketon and Stewart, unpublished). Rupprecht (1981) has shown that the males of some species of *Siphonoperla* (family Chloroperlidae) produce their signals by repeatedly jerking their bodies without abdomen/substratum contact. This method, termed tremulation (Busnel et al., 1956; Morris, 1980), also appears to be derived because other chloroperlid species produce the more typical beating type signals (Stewart and Zeigler, 1984a).

Exchange structure.—Exchange structure refers to the number of male and female signals in a typical drumming exchange and their arrangement. The simplest observed exchanges consist of a male call followed by a female answer. More complex is a three-way (or three-part since only two individuals are involved) exchange where a male response signal is added to the basic call-answer sequence. The presence of a response signal is most likely a derived character even though it is found in most families where drumming is known. Perhaps this character originated before many of the present families had diverged. We believe the male response signal must function to acknowledge receipt of the female's answer, thus establishing the certainty of communication contact for both partners and affecting proper behavior patterns (often including a cessation of locomotor activity in the female) for the duration of drumming contact. Rarer four- and five-part exchanges have also been observed (δ - δ - δ - δ and δ - δ - δ - δ - δ), but these often occur only in the first few exchanges of a longer exchange sequence (Zeigler and Stewart, 1985). Still, their occurrence could be important if certain families or genera uniformly lack them, as the Pteronarcyidae apparently do (Stewart et al., 1982a). The non-synchronous overlap of male and female signals within an exchange has been observed in some families (Fig. 8) and might also prove useful

if it is found to be common or totally lacking in certain groups.

Beat number/signal.—As mentioned above, this character can be highly variable both within and between species. However, there are instances where creating categories of number of beats/signal may be useful. For instance, male pteronarcyids produce calls ranging between 4–8 beats (Stewart et al., 1982a; Zeigler and Stewart, 1985), whereas males of the family Leuctridae produce calls of more than 20 beats (Zeigler and Stewart, 1977; Rupprecht, 1977). A large number of beats/signal has been suggested as a derived character state (Stewart and Zeigler, 1984b). In the perlids, this seems to be the case for the female answers of *Phasganophora capitata* (Pictet) (Maketon and Stewart, 1984) and *Paragnetina kansensis* (Banks) (Stewart et al., 1982b) which exceed 100 beats per signal (Fig. 10). To date, answers of other species rarely exceed 20 beats.

Beat intervals.—In the family Pteronarcyidae, at 22–25°C, *Pteronarcella* species produce signals with beat intervals of less than 130 msec, whereas *Pteronarcys* species produce signals with intervals greater than 200 msec (Stewart et al., 1982; Zeigler and Stewart, 1985). In most cases, the actual beat interval means (in msec) are probably too variable to be useful above the family level, and for diphasic calls, two such values must be reported (one/phase) making comparisons more difficult. However, there are other possible characters to be derived from beat interval measurements. As pointed out earlier, beat intervals can be constant throughout the signal, or they can increase (lengthen) or decrease (shorten) as the signal progresses. To date, the male call and female answer of all taeniopterygid species have increasing beat intervals, while peltoperlid signals have decreasing or constant beat intervals. Constant beat intervals, being the simpler situation, can be tentatively considered as the plesiomorphic condition.

Female calling.—In most stonefly species

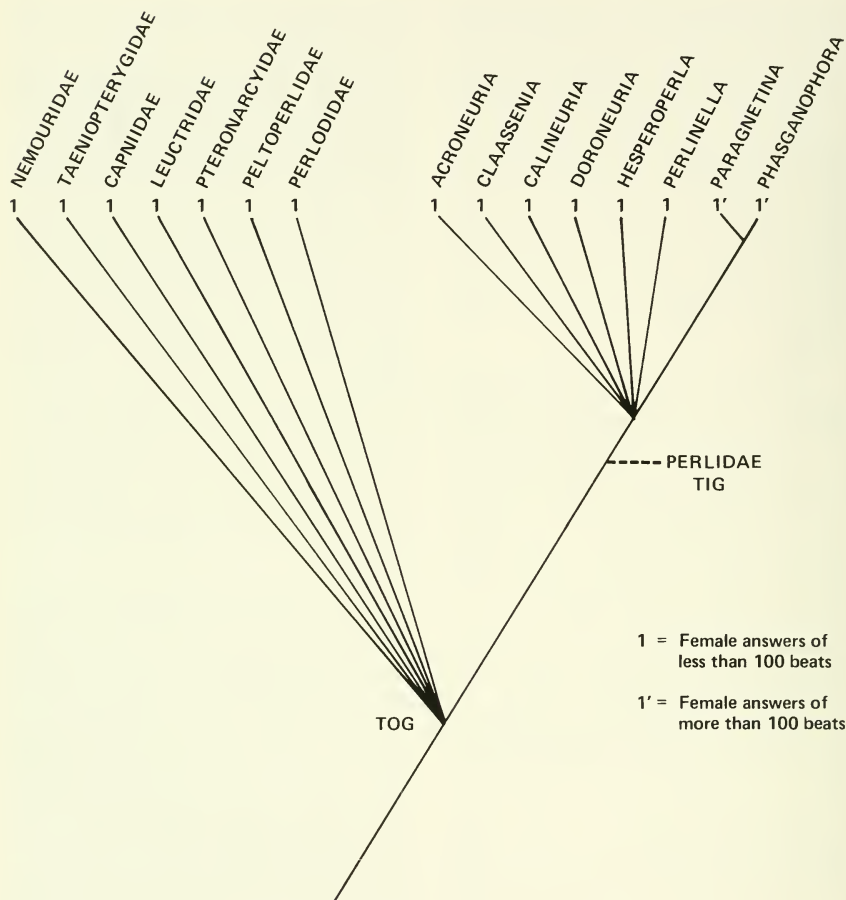


Fig. 10. Out-group comparison for female answers of more than 100 beats (TOG = taxonomic out-group, TIG = taxonomic in-group).

studied to date, the male initiates drumming communication with a calling signal. However, in some species of *Soliperla* (Stewart and Zeigler, 1984a) and *Doroneuria* (Maketon and Stewart, 1984) females will produce signals (calls?) in the absence of male drumming activity (though males do call in these species). Since this trait is apparently rare, it may prove to be apo-

morphic and to have some systematic value, or it may prove to be convergent in several genera due to some common set of environmental conditions. For example, calling in females would seem to be beneficial to a species which typically exists at low population densities, since calling by both sexes would effectively increase the chances for male-female contact where

drumming is a major mechanism for mate location.

CONCLUSIONS

Currently, drumming has been described for approximately 5% of the world Plecoptera fauna, currently estimated at around 1600 species (Arnett, 1983), and for some of these, only male signals have been obtained. Consequently, most of the ideas presented herein must be considered tentative. As the drumming of more species is elucidated, the systematic utility of these characters will be reinforced, weakened, or eliminated accordingly. Also, questions concerning the evolutionary rate in behavioral vs. morphological trends, as well as possible correlations between plesiomorphic/apomorphic character states in both areas, may be resolved.

Interestingly, the pteronarcyids, which are the most completely studied family (drumming descriptions for over 50% of the species) show several primitive drumming traits: monophasic calls, signal production exclusively by beating, few beats/signal, and lack of four- and five-part exchanges. This family exhibits many primitive morphological characteristics and is considered the most primitive extant group within its suborder (Nelson and Hanson, 1971). In contrast, the perlids, which are a diverse and relatively "derived group," exhibit many of the proposed apomorphic drumming characters discussed herein.

LITERATURE CITED

- Alexander, R. D. 1962. The role of behavioral study in cricket classification. *Syst. Zool.* 11: 53-72.
- Arnett, R. H. 1983. Status of the taxonomy of the insects of America north of Mexico, a preliminary report prepared for the subcommittee for the Insect Fauna of North America Project. Committee on Systematics Resources of the Entomological Society of America. R. H. Arnett, privately published. 49 pp.
- Busnel, R. G., B. Dumortier, and M. C. Busnel. 1956. Recherches sur le comportement acoustique des ephippigères (Orthoptères, Tettigoniidae). *Bull. Biol. Fr. Belg.* 3: 219-286.
- Henry, C. S. 1984. The sexual behavior of green lacewings, pp. 101-110. *In* Canard, M., Y. Semeria, and T. R. New, eds., *Biology of Chrysopidae*. W. Junk, The Hague.
- Maketon, M. and K. W. Stewart. 1984. Further studies of the drumming behavior of North American Perlidae (Plecoptera). *Ann. Entomol. Soc. Am.* 77: 770-778.
- Mayr, E. 1958. Behavior and systematics, pp. 341-362. *In* Roe, A., and G. G. Simpson, eds., *Behavior and Evolution*. Yale Univ. Press, New Haven.
- Morris, G. K. 1980. Calling display and mating behaviour of *Copiphora rhinoceros* Pictet (Orthoptera: Tettigoniidae). *Anim. Behav.* 28: 42-51.
- Nelson, C. H. 1984. Numerical cladistic analysis of phylogenetic relationships in Plecoptera. *Ann. Entomol. Soc. Am.* 77: 466-473.
- Nelson, C. H. and J. F. Hanson. 1971. Contribution to the anatomy and phylogeny of the family Pteronarcyidae (Plecoptera). *Trans. Am. Entomol. Soc.* 97: 123-200.
- Otte, D. and R. D. Alexander. 1983. The Australian crickets (Orthoptera: Gryllidae). *Acad. Nat. Sci. Phila. Mon.* 22: 1-477.
- Ross, H. H. 1974. *Biological Systematics*. Addison-Wesley Publishing Co., Inc., Reading, Mass. 345 pp.
- Rupprecht, R. 1967. Das Trommeln der Plekopteren. *Z. Vergl. Physiol.* 59: 38-71.
- . 1969. Zur Artsspezifität der Trommelsignale der Plekopteren (Insecta). *Oikos* 20: 26-33.
- . 1977. Nachweis von Trommelsignalen bei einem europäischen Vertreter der Steinfliegen-Familie Leuctridae (Plecoptera). *Entomol. Ger.* 3: 333-336.
- . 1981. A new system of communication within Plecoptera and a signal with a new significance. *Biol. Inland Waters* 2: 30-35.
- . 1982. Drumming signals of Danish Plecoptera. *Aquat. Insects* 4: 93-103.
- Stark, B. P. 1983. A review of the genus *Soliperla* (Plecoptera: Peltoperlidae). *Great Basin Nat.* 43: 30-44.
- Stewart, K. W., S. W. Szczytko, and B. P. Stark. 1982a. Drumming behavior of four species of North American Pteronarcyidae (Plecoptera): Dialects in Colorado and Alaska *Pteronarcella badia*. *Ann. Entomol. Soc. Am.* 75: 530-533.
- Stewart, K. W., S. W. Szczytko, B. P. Stark, and D. D. Zeigler. 1982b. Drumming behavior of six North American Perlidae (Plecoptera) species. *Ann. Entomol. Soc. Am.* 75: 549-554.
- Stewart, K. W. and D. D. Zeigler. 1984a. Drumming behavior of twelve North American stonefly (Plecoptera) species: First descriptions in Peltoperlidae, Taeniopterygidae and Chloroperlidae. *Aquat. Insects* 6: 49-61.

- . 1984b. The use of larval morphology and drumming in Plecoptera systematics, and further studies of drumming behavior. *Ann. Limnol.* 20: 105–114.
- Szczytko, S. W. and K. W. Stewart. 1979. Drumming behavior of four western Nearctic *Isoptera* (Plecoptera) species. *Ann. Entomol. Soc. Am.* 72: 781–786.
- Thornhill, R. and J. Alcock. 1983. *The Evolution of Insect Mating Systems*. Harvard Univ. Press, Cambridge, Mass. 576 pp.
- Watrous, L. E. and O. D. Wheeler. 1981. The out-group comparison method of character analysis. *Syst. Zool.* 30: 1–11.
- West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. *Quart. Rev. Biol.* 58: 155–183.
- Zeigler, D. D. and K. W. Stewart. 1977. Drumming behavior of eleven Nearctic stonefly (Plecoptera) species. *Ann. Entomol. Soc. Am.* 70: 495–505.
- . 1985. Drumming behavior of five stonefly (Plecoptera) species from central and western North America. *Ann. Entomol. Soc. Am.* 78: 717–722.
- Zwick, P. 1973. *Insect: Plecoptera. Phylogenetisches System und Katalog. Das Tierreich*, 94. Walter de Gruyter and Co., Berlin. 465 pp.